The effects of browntop (*Agrostis capillaris*) dominance after fire on native shrub germination and survival

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Abstract

The purpose of this study was to examine whether light competition affects the germination and establishment of indigenous shrub species under a browntop (*Agrostis capillaris*) canopy. Seeds from common, native shrub species (*Coprosma parviflora* and *C. propinqua* at Mt. Thomas, *C. pseudocuneata* at Cass, and *Ozothamnus leptophyllus*, *Discaria toumatou*, and *Leptospermum scoparium* at both sites) were sown into plots at Cass and Mt. Thomas that had been burnt between 1980 and 1996. The plots were blocked and randomly allocated to one of three treatments: control (no change), medium cut (grass cut to 10 cm) and short cut (grass cut to 5 cm). The germination rates varied greatly among species and sites, with the two smaller-seeded species (*O. leptophyllus* and *L. scoparium*) having lower germination than the rest. All of the shrub species experienced a significant treatment effect on germination, but the type of effect varied depending on the site conditions. It appeared that light competition alone was not limiting shrub germination. The density of shade cast by browntop and availability of water both appeared to be important in affecting shrub germination in this study. The results also show that shrub seed size, season of germination and probably between-year variation in summer rainfall could all be important factors in shrub recruitment.

Keywords: *Agrostis capillaris; Coprosma parviflora; Coprosma propinqua; Coprosma pseudocuneata; Discaria toumatou*; *Leptospermum scoparium;* light competition; *Ozothamnus leptophyllus*; seed germination

Introduction

Short-tussock grassland vegetation developed in many montane areas of the South Island when mountain beech forest was burnt at the end of the last century. These grasslands were initially dominated by *Festuca* tussocks, but over the last 50 years, many of these grasslands have been increasingly dominated by exotic grasses such as browntop (*Agrostis capillaris*) and flatweeds (Rose *et al.* 1995; White 1991). Although such fire-induced grasslands below the natural treeline are unlikely to be stable in the long-term (Calder *et al.* 1992), it remains unknown how these exotic grasses will affect successional processes that would eventually lead to the recovery of woody vegetation.

Wiser *et al.* (1997) suggest that in particular, areas adjacent to short-tussock grasslands now dominated by exotic grasses may receive exotic

seed inputs that can disrupt colonisation by native herbaceous and shrub species. Thus, while burns within beech forest matrices have largely been colonised by native herbs and shrubs (Cockayne & Calder 1932; MacDonald 1978), burns adjacent to grasslands may instead be dominated by exotic grasses such as browntop. At some high country sites, this dominance appears to be slowing the colonisation of native woody species (Wiser *et al.* 1997).

Competition from pasture grasses is known to limit the establishment of native shrubs and trees (Ministry of Forestry 1987), but it is not known what type of competition is most important in limiting shrub germination and survival. The purpose of this study was to examine whether light competition affects the germination and establishment of indigenous shrub species under a browntop canopy, whether light competition is more important than competition for other resources such as water or nutrients, and why this competition might be greater under exotic grass cover than in native grasslands.

Methods

This experiment was conducted at Cass and Mt. Thomas Forest, both high country sites in inland Canterbury. The study sites at Cass (600 m a.s.l.) were located on an alluvial fan below Sugarloaf next to the University Research Station and on Waterfall Terrace. The Sugarloaf site was last burnt by an accidental wildfire in 1996 and the Waterfall Terrace site was burnt by a wildfire in 1995. The Cass sites have been tussock or shrub communities in pastoral grazing since c. 1880 with the original mountain beech forest cleared in Polynesian fires about 600 years ago (Burrows 1977).

The two study sites in the Mt. Thomas Forest were located along the ridgeline track between Mt. Richardson and the Bypass Track to Glentui Picnic Area. One site was burnt in October 1980 and the other in 1993, both by accidental wildfires. Both sites are between 600 and 800 m a.s.l. The Mt. Thomas sites were mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest prior to the fire, but regeneration after the fire has been slow. By 1986, browntop covered between 55-95% of the ground area, while shrub cover was only 1-5% (Ministry of Forestry 1987). By 1995, succession was still slow and browntop still dominated both areas burnt in 1980 and 1993 (Wiser *et al.* 1997).

By 1999, shrub cover had increased somewhat at the 1993 burn site, but *Nothofagus* seedlings were not present at either study site (although they were present in other parts of the burnt area) and browntop still dominated.

Fifteen plots (1 m^2) were established at each of the four study sites. The plots were blocked in sets of three to minimise differences in soil and vegetation across each site. Within each block, plots were randomly allocated to one of three treatments: control (no change), medium cut (grass cut to 10 cm) and short cut (grass cut to 5 cm). Seeds from common, native shrub species (*Coprosma parviflora* and *C. propinqua* at Mt. Thomas, *C. pseudocuneata* at Cass, and *Ozothamnus leptophyllus*, *Discaria toumatou*, and *Leptospermum scoparium* at all sites) were collected in April from plants at each site. All seeds were collected locally except for *D. toumatou*, which was collected from Cass only but sown into all sites (local seeds were not available at Mt. Thomas). Prior to sowing, the flesh was removed from *Coprosma* seeds, and *L. scoparium* and *D. toumatou* seeds were removed from their capsules.

When *Coprosma parviflora, C. propinqua*, and *C. pseudocuneata* seeds were prepared for sowing, a large number of seeds were observed to be infected by a disease or predator that created a small black hole on the seed case and turned the inside of the seed black. To determine if these discoloured seeds could germinate, 3 trays of 20 affected *C. propinqua* seeds and 2 trays of 20 discoloured *C. pseudocuneata* seeds were also planted in the glasshouse.

Seeds were planted on 14-15 April 1999 into a 100 cm^2 marked area in the middle of each field plot. In every plot, 550 *O. leptophyllus* seeds, 20 *D. toumatou* seeds, and 2025 *L. scoparium* seeds were sown. At Mt. Thomas, 20 *C. parviflora* seeds and 20 *C. pseudocuneata* seeds were also sown, while 20 *C. propinqua* seeds were sown in the Cass plots. In addition, four trays of seeds of each species (the same number as sown in each plot) from Cass and Mt. Thomas were placed in a glasshouse. Germination and survival of these seeds was recorded every two months, and these rates were compared to the field results.

Every two months, the plots were checked for seed germination and the grass cover was cut to the appropriate height. Two plots at the Mt. Thomas 1993 site were destroyed by wild pigs during the study and these plots were excluded from analysis. The final data were recorded in January 2000, nine months after sowing. Percent germination and survival were compared for each species between sites, treatments, and blocks using a generalised linear model with a binomial distribution on S-Plus. F-tests were used rather than Chi-square tests to give a better fit to the model.

Results

Figure 1a) shows the timing of seed germination in the field. Both *L. scoparium* and *O. leptophyllus* began germinating in the autumn shortly after

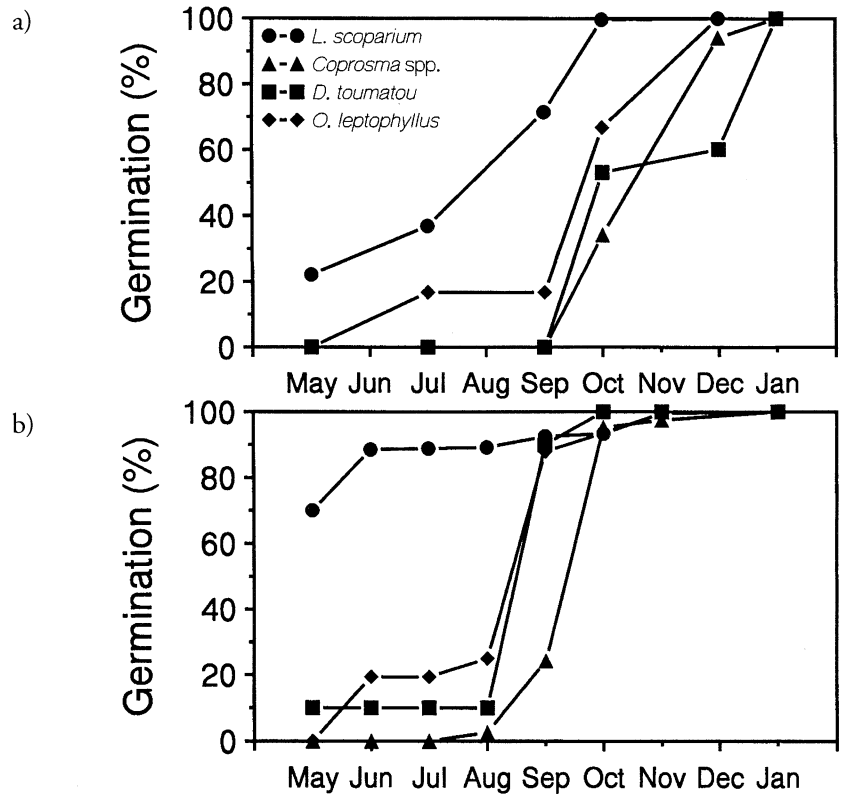

Figure1. Cumulative germination of seeds of *Ozothamnus leptophyllus, Coprosma* spp., *Discaria toumatou,* and *Leptospermum scoparium* a) sown in the field at Cass and Mt. Thomas, and b) sown in the glasshouse from May 1999 until January 2000. Germination was combined for each species across sites and for the three *Coprosma* species because these rates were similar.

Table 1. Germination (%) of seeds of *Ozothamnus leptophyllus*, *Coprosma* spp, *Discaria toumatou* and *Leptospermum scoparium* sown at four field sites in 1999 and in the glasshouse.

	Cass Sugar-loaf fan	Cass Waterfall Tce	1980 Mt. Thomas burn	1993 Mt. Thomas burn	Glasshouse seeds from Cass	Glasshouse seeds from Mt. Thomas
O. leptophyllus	0.05	0.02	0.07	0	0.73	15.55
C. parviflora	-	-	11.67	5.77	-	8.75
C. propinqua	16.00	15.00	-	-	16.25	-
C. pseudocuneata	-	-	16.00	12.31	-	18.75
D. toumatou	6.00	4.33	14.33	4.23	25.00	-
L. scoparium	0.09	0.14	0.40	0.35	14.99	14.94

seeds were sown, presumably because these small-seeded species do not have a dormancy mechanism (Burrell 1965). None of these seedlings survived until the following summer. In contrast, *Coprosma* spp. and *D. toumatou* seeds did not begin germinating until September, and many of these seedlings survived through January.

The germination rates varied greatly among species and sites, with the two smaller seeded species (*O. leptophyllus* and *L. scoparium*) having lower germination than the other species (Table 1). *O. leptophyllus* germinated the least in the field (0-0.7%) and germination was much higher in the glasshouse (0.7% of Cass seeds and 15.6% of Mt. Thomas seeds). *L. scoparium* also had low germination rates in the field (0.1-0.4%) and higher germination in the glasshouse (15% of seeds from both sites). Germination rates for the three *Coprosma* species were similar in the field and the glasshouse and ranged from almost 6% to almost 19%. *D. toumatou* had the highest germination rate in the glasshouse (25% of Cass seeds) but germinated less in the field (4 to 14%; Table 1).

O. leptophyllus germination was significantly different among the field sites ($F = 4.18$, $p = 0.028$) and among the treatments ($F = 25.72$, $p < 0.001$), and the interaction effect between site and treatment was also significant ($F = 5.17$, $p = 0.004$). No seeds germinated at the 1993 Mt. Thomas burn, while the most germination occurred at the 1980 Mt. Thomas burn (0.07%; Table 2a). At both Cass sites, germination only occurred in plots with the short cut treatment. Germination at the 1980 Mt. Thomas burn was the same in medium and short cut plots but zero in the control plots (Table 2a).

The treatment effect was also significant for each of the three *Coprosma* species (*C. parviflora* $F = 3.84$, $p = 0.047$; *C. propinqua* $F = 5.07$, $p = 0.021$; *C. pseudocuneata* $F = 17.10$, $p < 0.001$), although there was no significant difference in germination among field sites for each species.

Table 2. Percent germination of a) *Ozothamnus leptophyllus* seeds sown at the four field sites in the three treatment categories; b) *Coprosma parviflora* and *C. pseudocuneata* seeds sown at Mt. Thomas and *C. propinqua* sown at Cass; c) *Leptospermum scoparium* seeds sown at the four field sites; and d) *Discaria toumatou* seeds sown at the four field sites.

a)

	1980 Mt. Thomas burn	1993 Mt. Thomas burn	Cass Waterfall Tce	Cass Sugarloaf Fan
Control	0	0	0	0
Medium cut	0.11	0	0	0
Short cut	0.11	0	0.07	0.15

b)

	C. parviflora	*C. pseudocuneata*	*C. propinqua*
Control	17.2	35.6	7.5
Medium cut	9.4	8.3	19.5
Short cut	1.0	0.50	19.5

c)

	1980 Mt. Thomas burn	1993 Mt. Thomas burn	Cass Waterfall Tce	Cass Sugarloaf Fan
Control	0.19	0.44	0.02	0
Medium cut	0.52	0.31	0.15	0.04
Short cut	0.49	0.31	0.24	0.24

d)

	1980 Mt. Thomas burn	1993 Mt. Thomas burn	Cass Waterfall Tce	Cass Sugarloaf Fan
Control	21.0	3.8	2.2	0
Medium cut	6.0	3.8	3.3	3.0
Short cut	16.0	5.0	7.0	15.0

The two species sown at Mt. Thomas (*C. parviflora* and *C. pseudocuneata*) germinated most in the control plots and least in the short cut plots, while *C. propinqua* at Cass germinated equally well in the short and medium cut plots but worst in the control plots (Table 2b).

L. scoparium germination also differed significantly between treatments ($F = 3.93$, $p = 0.031$) and between sites ($F = 9.41$, $p < 0.001$), and the site/treatment interaction effect was significant ($F = 3.23$, $p = 0.014$). Germination was better at the Mt. Thomas sites than at the Cass sites (Table 2c). At the two Cass sites, germination was best in the short cut plots and

Table 3. Percent survival of seeds that germinated at the four field sites and in the glasshouse until January 2000. The number of seeds that germinated at each site is in brackets.

	Cass Sugar-loaf fan	Cass Waterfall Tce	1980 Mt. Thomas burn	1993 Mt. Thomas burn	Glasshouse seeds from Cass	Glasshouse seeds from Mt. Thomas
O. leptophyllus	0 (4)	0 (2)	0 (6)	0 (0)	56.3 (16)	89.7 (342)
C. parviflora	n/a	n/a	4.7 (35)	18.0 (15)	n/a	100 (7)
C. propinqua	20.9 (48)	35.9 (45)	n/a	n/a	70.8 (13)	n/a
C. pseudocuneata	n/a	n/a	38.7 (48)	19.0 (32)	n/a	87.5 (15)
D. toumatou	17.8 (18)	46.7 (13)	48.4 (43)	38.5 (11)	79.2 (10)	n/a
L. scoparium	0 (28)	0 (44)	0 (122)	0 (91)	84.2 (1214)	81.9 (1210)

worst in the control plots. In contrast, at the 1993 Mt. Thomas burn site, germination was best in the control plots and worst in the short cut plots. Germination at the 1980 Mt. Thomas burn site was best in the medium cut plots and worst in the control plots (Table 2c).

Germination of *D. toumatou* seeds was also significantly different among treatments ($F = 3.79$, $p = 0.034$) and among sites ($F = 4.63$, $p = 0.009$). The 1980 Mt. Thomas burn site had significantly more germination than the other sites (Table 2d). At this site, germination was best in the control plots, also good in the short cut plots and lowest in the medium cut plots. At the other three sites, germination was lower overall, and was highest in the short cut plots and lowest in the control plots (Table 2d).

Average survival rates were better for all species in the glasshouse than in the field (Table 3). No *O. leptophyllus* and *L. scoparium* seedlings survived in the field until January 2000, whereas both survived well in the glasshouse. All of the large-seeded species had some seedlings (5-48%) still alive in the field in January 2000, but again survival was highest in the glasshouse (71-100%). Survival rates were not significantly different among the field sites for *D. toumatou* ($F = 0.89$, $p = 0.46$), *C. parviflora* ($F = 5.24$, $p = 0.06$), *C. propinqua* ($F = 1.66$, $p = 0.21$), and *C. pseudocuneata* ($F = 0.13$, $p = 0.72$). *O. leptophyllus* and *L. scoparium* had no survival in the field. None of the species with surviving seeds experienced a significant treatment effect on survival and there was no consistent pattern in survival rates in different treatments among species (Table 4).

Discussion

The oldest site (the 1980 Mt. Thomas burn site) had the highest germination rate for every species; germination among the field sites varied

Table 4. Percent survival of seeds that germinated in the three treatment classes (all study sites combined), and the treatment effect for each species.

	Control	Medium cut	Short cut	F-statistic (p-value)
O. leptophyllus	0	0	0	--
C. parviflora	55.56	37.04	10.00	0.69 (0.54)
C. propinqua	26.00	21.51	37.60	1.95 (0.17)
C. pseudocuneata	42.96	37.78	10.00	0.99 (0.41)
D. toumatou	33.33	22.50	57.17	1.90 (0.18)
L. scoparium	0	0	0	--

significantly for *D. toumatou*, *L. scoparium*, and *O. leptophyllus*. It is possible that the suitability of burn sites for shrub seeds may improve as time since the fire increases. However, this interpretation is based on only one older site and other site characteristics may have also contributed to the difference in germination. In addition, with one exception (*O. leptophyllus* at the Mt Thomas 1993 site) all species germinated at all sites.

All of the shrub species experienced a significant treatment effect, but the type of effect varied. *O. leptophyllus* had a low germination rate overall, with no seeds germinating at the 1993 Mt. Thomas burn and less than 1% of the Cass seeds germinating even in the glasshouse. This species may primarily reproduce vegetatively rather than through seed or it may require bare soil for germination. This species was unique in having higher germination in cut plots than in control plots at all sites. The low germination percentages from the Cass site may indicate some problem with pollination, either due to weather during the year of the study, or to an absence of suitable pollinators. *O. leptophyllus* has typical small Asteraceae capitula which, like most New Zealand flowers, are thought to be visited by a range of non-specialised insects (Webb & Kelly 1993), so recurrent pollinator limitation should be unlikely.

Germination rates for the remaining species were highest under varying treatments depending on the site conditions. The height and density of browntop varied among plots and may have contributed to variations in seedling germination. In general, the uncut grass was more dense at Cass than at Mt. Thomas, which could partially explain why species tended to germinate more often in the control and medium cut plots at Mt. Thomas than in control and medium cut plots at Cass.

In addition, the effects of browntop on native shrub regeneration are influenced by a range of other factors, including aspect, climate, and nutrient and water availability. For example, the Mt. Thomas sites were on northwest-facing slopes, and the frequent gale force fohn winds from the north-west that sweep across the ridgeline have a drying effect that may limit establishment in open sites. At such sites, grass cover may actually protect some seeds and seedlings from desiccation. In contrast, the Cass sites have slight eastern (Waterfall Terrace) and western (Sugarloaf Fan) aspects, and they are

protected from the dominant winds by adjacent areas of dense shrub cover. Therefore, at Cass moisture is probably less limiting, and areas with cut vegetation may provide good establishment sites for native species. These complex effects are likely to have an even greater effect on survival than on germination, but not enough seeds survived for statistically significant effects to be noted.

In general, the effects of other vegetation are likely to be a mixed blessing for seed germination and seedling establishment. Deep shade is harmful, but direct sunlight can lead to heat stress, greater water loss from the seedling, drying of the upper soil layers, and photoinhibition. Cover may also have an effect via root competition, with taller competing vegetation reducing nutrient and water availability in the upper soil layers, especially where the competing vegetation is a grass with the typical dense graminoid root system. Therefore, seed germination and establishment would be expected to be best in microsites that are protected from extremes of sunshine and dry soil but do not experience excessive shading or root competition.

Different plant species may have different optimum conditions, depending on their season of germination, levels of shade and drought tolerance, and association with mycorrhizae. Evidence supporting this hypothesis includes work done in the Cass area on establishment of beech (*Nothofagus*) seedlings by Easterbrook (1998). Easterbrook showed that shading reduced death rates of transplanted seedlings, but also reduced growth rates. In grasslands in the southern South Island, Lee *et al.* (1993) showed that the greatest number of surviving seedlings of the snow tussock *Chionochloa rigida* were 0.5-1 m from the parents, where they were shaded and protected from grazing by the canopy of the adult tussock. The optimum microsites for both germination and survival of several short lived herbs in British chalk grasslands were shown to be at an intermediate level of shading (Kelly 1989).

If the exact levels of light and water competition are both important for native shrub establishment, the structural differences between exotic grass communities and native tussock grasslands are of primary importance. Several authors have commented on the denser, more vigorous growth of introduced grasses and on how this growth appears to change the structure of native grasslands (White 1991; Wiser *et al.* 1997). The original native grassland provided a mosaic of tall tussocks, with shade under the canopies separated by open spaces, supporting a range of inter-tussock species. The edge of the canopies was the microhabitat where Lee *et al.* (1993) found most *Chionochloa rigida* seedlings.

White (1991) noted that with the spread of browntop, the grasslands at Cass became less diverse and there was a reduction in native inter-tussock herbs. These same changes could reduce the number of microsites suitable for establishment of native shrubs and trees (Wiser *et al.* 1997; Easterbrook 1998). However, our data show that clipping browntop to shorter sward heights does not consistently improve germination or survival of six native shrubs, suggesting that simple light competition is not the sole means by which browntop restricts establishment of woody species. Interactions with other factors (shade sensitivity of each shrub species, rainfall levels during the study, season of germination, and site aspect) may also influence shrub establishment and growth. Alternatively, clipping browntop may not create microsites that are as suitable as those under the edge of tussock grasses. Clipping browntop will reduce shading, but it may not significantly ameliorate root competition and it may actually increase water stress on seedlings.

Short tussock grasslands may provide "safe sites" for shrub establishment by providing regions between plants that have adequate light levels yet are also protected from moisture loss. In contrast, exotic grasses such as browntop tend to form dense swards that limit light levels across large areas, and if these grasses are cut, the ground

is then exposed to rapid moisture loss. These differences may partially explain why the succession of native shrublands after fire is limited by the dominance of exotic grasses. The effects of browntop cannot be ascribed solely to light competition. Interactions with root competition and water relations are probably also important. The results also show that shrub seed size, season of germination and probably between-year variation in summer rainfall could all be important factors in shrub recruitment.

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References

Burrell, J. (1965). Ecology of *Leptospermum* in Otago. *New Zealand Journal of Botany* 3: 3-16.

Burrows, C.J. (1977). *History and science in the Cass District, Canterbury, New Zealand.* Department of Botany, University of Canterbury, Christchurch, New Zealand.

Calder, J.A., Bastow Wilson, J., Mark, A.F., & Ward, G. (1992). Fire, succession and reserve management in a New Zealand snow tussock grassland. *Biological Conservation* 62: 35-45.

Cockayne, L. & Calder, J. W. (1932). The present vegetation of Arthur's Pass (New Zealand) as compared with that of 34 years ago. *Journal of Ecology* 20: 270-283.

Easterbrook, M. J. (1998). *Micro-habitat dependent spread of* Nothofagus solandri *into non-forested habitats.* Unpublished M.Sc. thesis, University of Canterbury, Christchurch, New Zealand.

Kelly, D. (1989). Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. *Journal of Ecology* 77: 770-784.

Lee, W. G., Fenner, M. & Duncan, R. P. (1993). Pattern of natural regeneration of narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* in Central Otago, New Zealand. *New Zealand Journal of Botany* 31: 117-125.

MacDonald, M. C. (1978). Mount Reeves. *Wellington Botanical Society Bulletin* 40: 31-33.

Ministry of Forestry. (1987). Reforestation after fire in Canterbury beech forests. *What's new in forest research* 149.

Rose, A.B., Platt, K.H., & Frampton, C.M. (1995). Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* 19(2): 163-174.

Webb, C.J., & Kelly, D. (1993). The reproductive biology of the New Zealand flora. *Trends in Ecology and Evolution* 8: 442-447.

White, E. G. (1991). The changing abundance of moths in a tussock grassland, 1962-89, and 50- to 70-year trends. *New Zealand Journal of Ecology* 15: 5-22.

Wiser, S.K., Allen, R.B., & Platt, K.H. (1997). Mountain beech forest succession after a fire at Mt. Thomas Forest, Canterbury, New Zealand. *New Zealand Journal of Botany* 35: 505-515.